Urban densification reduces food-web robustness despite partial gains through local habitat improvements

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Abstract

Urban densification is widely promoted to curb sprawl, yet the replacement of existing green infrastructure threatens species across multiple trophic levels. Species are embedded in complex food webs, and understanding how densification restructures urban food webs is essential for predicting functional change and evaluating whether local habitat improvements (e.g. greater vegetation diversity) can yield cascading effects across trophic levels. Using a metaweb approach and empirical information on species co-occurrences, we inferred multi-trophic food webs for 84 gardens in Zurich, Switzerland, selected along two largely independent gradients: landscape-scale urban densification, and local habitat quality. Densification decreased primary consumer and predator richness, decreasing food web connectance, generality and modularity. It also reduced structural robustness to secondary extinctions (R_{coef}) but not the network collapse threshold R_{50}. Improved local habitat quality increased primary consumer and predator richness as well as null-standardised degree skewness, and indirectly increased R_{50}, but not R_{coef}. Our findings indicate that local habitat improvements within individually managed gardens alone are unlikely to maintain the structural robustness of food webs to densification. Maintaining connected, high-quality green infrastructure across the urban landscape will also be necessary to sustain robust food webs and their contributions to city dwellers.

Introduction

Cities represent the world's fastest growing novel ecosystems, where communities and food webs assemble under unprecedented conditions [1]. Many cities host surprisingly high levels of biodiversity—including rare and endangered species [2]—within remaining open spaces that are at least partially covered by vegetation (urban green spaces). The interactions among species from different trophic levels within the novel communities of these urban green spaces also provide crucial ecosystem services, including pest control, seed-dispersal and pollination [3–5], to over half the global human population [6]. Urban densification strategies—such as in-fill development and urban consolidation—have been widely promoted for sustainable development, minimising the net negative effects of habitat loss on biodiversity and ecosystem functions [7]. As a result, urban green spaces, their biodiversity, and their functionality are themselves increasingly threatened by densification initiatives [8,9]. Sustainable densification will therefore require urban planning that allows existing green spaces and their ecological functionality to persist. Consequently, understanding the structure and stability of urban food webs has become both a fundamental ecological question and an emerging conservation priority.

Urban densification does not affect all species equally; where some bees [10] and predatory wasps [11] may increase in diversity, predators, especially ground invertebrates, have declined [10,12,13]. Subsequently, densification may have functional consequences for urban ecosystems through the loss of not only species [9], but also the interactions between them [14,15]. Indeed, local interactions may be lost more rapidly than the species themselves: declining population densities can reduce encounter rates, and the loss of interaction partners prevents otherwise persisting species from fulfilling their ecological roles, leading to a decline in ecosystem services far before the species themselves are lost [14]. Emerging work on urban multi-trophic networks has shown that predator decline alters food web structure [13] and decreases food web robustness (the capacity to withstand secondary extinctions) [16] in urban green spaces. However, urban multi-trophic network approaches

64 often aggregate species into broad functional categories or guilds, limiting our ability to
65 understand how densification affects urban ecosystems structured by simultaneous species-
66 level bottom-up and top-down processes [17,18]. Recent calls have emphasised the
67 underutilised potential of integrating food web metrics into conservation planning [19]. For
68 example, preventing secondary extinctions through the identification of vulnerable predators
69 or prey is an efficient approach that allows a focus towards fewer species while
70 simultaneously preventing cascading effects on the community [19]. Accordingly, a multi-
71 trophic food-web perspective can be useful to quantify how urban densification impacts
72 ecological interactions and stability in urban green spaces.

73 Intensive urban land use constrains ecological communities by reducing total habitat
74 quantity, quality and connectivity across spatial scales [20]. Landscape-scale habitat loss
75 can impact, in particular, higher trophic levels by reducing predator diversity, leading to the
76 emergence of food webs that are more connected and less nested [13] and potentially
77 compromise food web stability [21]. Furthermore, intensive maintenance of urban green
78 spaces can operate strong bottom-up controls at the local habitat patch scale, typically by
79 regular mowing and removal of herbaceous vegetation, whereby refugia, nesting sites and
80 basal dietary resources (e.g., detritus) are removed [22]. In sharp contrast, the composition
81 of spontaneous plant communities and cultivated assemblages are directly shaped by
82 design and management decisions, and have been shown to promote the diversity of
83 herbivores [23], pollinators [15,24] and decomposers [25], with positive effects on ecosystem
84 services [15]. Other local improvements—such as management extensification and
85 promotion of habitat diversity—can promote taxonomic [25,26] and functional diversity [27],
86 especially that of predators [28], with indirect consequences for food web structure, such as
87 more modularity, nestedness and omnivory [13], the latter likely stabilising food webs [29].
88 Overall, these empirical findings align well with the intermediate landscape-complexity
89 hypothesis, which postulates that in relatively simplified and intensified landscapes, targeted
90 local management could partially buffer the negative effects of anthropogenic pressure in the

91 surrounding landscape [30]. Applied to urban ecosystems, this framework suggests that
92 local habitat management may be successful at intermediate levels of urban densification .

93 Urban gardens provide a unique opportunity to evaluate whether improving local habitat
94 quality can counteract the structural simplification of food webs associated with urban
95 densification. Making up around 20% of green spaces in European cities [31], they face
96 increased risks of being removed under densification strategies, being less profitable in
97 comparison to other green spaces [32]. This is particularly true for publicly-owned allotments
98 [32], which provide crucial services to underprivileged city-dwellers in the form of
99 subsistence food production and access to nature [33], while also often being richer in plant
100 species [34]. In non-urban contexts, plant diversity has been demonstrated to promote food
101 web complexity [35], plant-insect interactions and associated ecosystem services [36].
102 Indeed, flowering-species rich urban gardens have been shown to maintain the abundance
103 of some pollinator groups and pollination success along an urban density gradient [15].
104 However, determining whether these benefits extend across trophic levels requires
105 information on how the species occurring in gardens are connected within food webs.

106 Empirical observations of multi-trophic interaction networks in urban gardens remain scarce
107 (but see [13]), and difficult to obtain. Yet a recently published database of species-level
108 trophic interactions [37] as well as increasing implementation of the meta-food web
109 (henceforth metaweb) approach allows comprehensive and standardised comparisons of
110 food webs [38] in hitherto understudied urban systems. A metaweb is a potential pool of
111 regional interactions, which can be combined with knowledge of local species co-
112 occurrences to infer local food webs [39]. In this study, we used empirically inferred food
113 webs from 84 gardens across Zurich, Switzerland, selected along two independent gradients
114 of urban density and local habitat quality. We asked: (1) How do local habitat quality and
115 landscape-scale urban density influence the compositional and structural properties of multi-
116 trophic garden food webs? (2) Can improvements in local habitat quality and subsequent
117 shifts in network structure buffer food-web robustness to species loss? (3) Do the effects of

local habitat quality and urban densification on food-web structure and robustness emerge indirectly through changes in trophic composition, particularly predator richness?

Methods

Study area and design

We selected 85 urban gardens along a double, quasi-orthogonal gradient of landscape-scale urban density and local structural vegetation complexity in the city of Zurich, Switzerland (Fig. 1A). The study area and sampling design have been extensively detailed in earlier studies [11,40]. Gardens were spatially distributed to ensure a representation of all urban districts and maximise independence between the two environmental gradients.

We selected 43 private and 42 allotment gardens; one allotment garden was excluded as the management intensity survey could not be completed. Private gardens are directly adjacent to either a single-occupancy or terraced house and allotment gardens are public clustered garden lots managed by associations, but leased to leisure gardeners [41]. Gardens were selected based on the habitat map of Zurich [42], aerial images and through field visits [40]. Gardens were selected with regards to the urban density gradient as the proportional area of built-up surface within a 500-m radius around each garden [40]. Gardens had a median pairwise distance of 4.5 km (IQR: 2.9–6.1 km; range: 0.1–10.8 km).

Predictors

Urban density was calculated as the first axis of a principal component analysis (PCA) collapsing several urban markers corresponding to three well-established dimensions of landscape-scale habitat needs: quantity, quality, and connectivity [20] around a 500-m buffer around the garden sites. These comprised impervious surface cover and its temporal change [43,44], building height, green-patch cohesion, distance to forest and water, habitat-type richness, vegetation-height heterogeneity and the proportion of high-NDVI vegetation

143 [45] (Table S1). A combination of multiple spatial scales (from 50-m to 1-km) are best used
144 to adequately capture the variation in species composition in urban green spaces in the
145 same city [28]. However, as multiple other studies in these sites have demonstrated high
146 correlation of densification variables, with virtually identical responses across other models
147 [15,26], we elected to only focus on the 500-m scale, as it is commonly used in other studies
148 in Zurich [13,27]. The first PC (50.7% of variance) described a strong gradient from
149 structurally complex and connected vegetation with high diversity and NDVI to low
150 connectivity sites with taller buildings, and more impervious surface (Fig. S1).

151 Local habitat quality was calculated as the first axis of a PCA incorporating key drivers which
152 have been quantified in earlier studies [27]. This included the management intensity index,
153 which was developed to be a standardised, cumulative metric based on the frequency of
154 common garden and horticultural activities affecting the soil and various layers of vegetation,
155 including leaf litter, grasses, shrubs, and trees [46]. This specific index has been
156 demonstrated to well-explain biodiversity patterns of different taxonomic groups in previous
157 studies [11,47]. We additionally incorporated structural diversity (Shannon diversity of land
158 cover types [27]), relative cover of water and detritus, and Shannon diversity of vascular
159 plant species, within the gardens, based on a comprehensive 2015 inventory [40]. The first
160 PC (40.1% of variance) describes a 'local habitat quality' gradient moving from intensively
161 managed gardens with low habitat structural diversity to gardens with high habitat structural
162 and plant diversity, with increased relative cover of leaf litter and water (Fig. S1).

163 ## Biodiversity sampling

164 All biodiversity sampling was conducted in multiple surveys within the *Better Gardens* project
165 and carried out in the city of Zurich, Switzerland between 2015 and 2016. Here, we
166 synthesised the combined occurrence data collected over the study period (Fig. 1B).

167 Vascular plants were surveyed across entire garden lots throughout the 2015 growing
168 season and supplemented with vegetation relevés from two 10 m^2 quadrats per garden [40].

Surface-dwelling and flying arthropods were sampled in the summer of 2015 using pitfall and pan traps [27], respectively, while parasitoids and kleptoparasites were collected from trap nests deployed between February and October 2016 [11]. Invertebrates were sorted in the laboratory and identified by taxonomic experts. Further details are available in the SI and [27].

Metaweb and local garden food web inferences

We constructed the city-level metaweb primarily from the existing Swiss metaweb [37], supplemented with literature-driven interactions for under-represented groups such as horticultural plants (Table S2). The metaweb was collapsed to the genus-level; this resolution has been shown to capture trophic dynamics along environmental gradients while reducing taxonomic biases arising from uneven knowledge on interactions at the species-level [48,49]. We additionally included previously defined [37] non-vascular-plant basal resources as feeding guilds which were universally available (e.g. microbes, detritus). The final metaweb consisted of 17,314 interactions between 1,210 genera and 22 feeding guilds (Fig. 1C).

Local garden-level food webs (henceforth: local web) were inferred by filtering interactions from the metaweb to taxa that co-occurred in each garden based on biodiversity sampling [39] (Fig. 1D). To generate baseline expectations for network structure, we built 1,000 constrained null webs for each local web, in which the observed number of taxa and links were preserved (details in SI). The structure of local webs differed significantly from null expectations (Fig. S3).

We quantified several common food web properties for each local web. We considered the richness of primary consumer nodes (trophic level = 2) and higher-order consumer nodes (trophic level > 2, henceforth: predators). We also selected network properties that summarise their composition and structure. The compositional metrics included mean trophic level, node degree skewness, generality and omnivory. The structural metrics were

modularity and nestedness, properties that have been linked to network stability [50] (see glossary in Table S3). As these metrics are known to scale with network size and link density [51], we expressed node degree skewness, nestedness and modularity as z-scores relative to the null-model networks.

Robustness analyses

We quantified robustness, the capacity of a local web to maintain its structure and functioning while undergoing primary species extinctions [52]. As plants in gardens are directly managed by gardeners, we only simulated the loss of animal genera. Extinctions proceeded stepwise, with one animal genus removed at each step under one of two scenarios.

In the random scenario, each remaining animal has equal removal probability, providing a baseline against which to compare the second, more realistic scenario. In the second scenario, removal probabilities were weighted according to genus-specific sensitivity to urban density, estimated from occupancy-model β coefficients (SI). A scaling parameter *k* controlled the strength of the sensitivity weighting; results were insensitive to the values tested (Fig. S2). After each primary removal, we triggered secondary extinctions by repeatedly deleting consumer taxa that lost all available resources, until no further consumers met the extinction criteria. At each step, we recorded the number of remaining animal taxa, the number of weakly connected components (WCC), and the size of the largest WCC in the undirected version of the web. WCC are defined as fully isolated sub-networks within a food web, representing network fragmentation, which may restrict energy and material flow between species across the sub-networks [53], while the largest WCC represents the largest of the isolated sub-networks.

Robustness was quantified using two complementary metrics representing species loss and structural fragmentation. Robustness coefficient (R_{coef}) measures the area under the curve describing the decline of the largest WCC as species are sequentially removed, scaled to

the idealised linear-loss scenario; lower values represent faster structural collapse [54]. Changes in the largest WCC provide a measure of robustness to sustained extinctions across a variety of complex real-world networks [54], including food webs [55]. Collapse threshold (R_{50}) measures the proportion of primary removals required for the web to decline to half its initial size [56]. The two robustness metrics were positively correlated but not interchangeable (Fig.S6). Since simulations ended once all animals were removed, R_{50} was calculated relative to the total number of animal taxa rather than all taxa in each web. Each garden was simulated 1,000 times under all extinction scenarios.

Statistical analyses

To examine how trophic composition and structure varied along local and landscape environmental gradients, we fitted linear models to standardised measures of primary consumer richness, predator richness, mean trophic level, node degree skewness, generality, omnivory, modularity, and nestedness. For each metric, we modelled variation as a function of urban density, local habitat quality, garden area, and garden type (private vs. allotment). To test whether urban density affected primary consumers and predators differently, we additionally fitted a joint Poisson generalised linear mixed model to raw richness counts, including trophic group and its interactions with urban density, local habitat quality, garden area, and garden type, with garden identity as a random intercept to account for paired richness responses from the same garden. All other models assumed approximate Gaussian errors and met assumptions of homoscedasticity and normality based on residual diagnostics. Gaussian models were retained for consistency across response variables; richness models were additionally checked using Poisson and negative-binomial error distributions, with qualitatively consistent results (SI; Table S7).

To test how robustness responded to environmental gradients under each extinction scenario, we modelled the replicate means of R_{coef} and R_{50} using β generalised linear models (β-GLM). Models were fitted separately for random and urban-sensitivity extinction

scenarios. For each model, we included urban density, local habitat quality, and their interaction as fixed effects, with garden type and relative garden area included as additional covariates to account for local-scale variation.

To disentangle direct and indirect pathways linking environmental gradients to food-web structure, composition, and robustness, we fitted piecewise structural equation models (SEMs, Fig. S8). Based on well-knowledge relationships from the literature [16,51], we constructed two complementary SEMs: one focusing on network structure (nestedness, modularity, R_{coef}), and one on network composition (degree skewness, mean trophic level, generality, omnivory, and R_{50}). Each SEM consisted of a set of linear submodels fitted at the garden level. Urban density and local habitat quality were included as exogenous predictors in all relevant submodels. Predator richness was modelled as an intermediate predictor linking environmental gradients to downstream food-web properties. Structural metrics (nestedness and modularity) and node degree skewness were expressed as z-scores relative to null-model expectations to control for network size and link density, whereas the other compositional metrics (omnivory and mean trophic level) were analysed as standardised raw values. Because generality is expected to increase with taxonomic richness, we used richness-corrected generality (henceforth: residual generality), calculated as the residuals from a linear model relating generality to taxonomic richness. Garden area and garden type were excluded from the final SEMs to reduce model complexity, after sensitivity analyses showed that their inclusion did not alter the effects of urban density or local habitat quality (SI; Fig. S10). To quantify the relative importance of direct versus indirect pathways, we extracted standardised path coefficients from each SEM and calculated indirect effects as the product of component paths. Uncertainty around direct, indirect, and total effects was estimated using parametric bootstrapping (10,000 resamples), drawing from the estimated coefficient distributions of the fitted submodels.

All statistical analyses were conducted in R version 4.3.2 [57]. Linear models were implemented using *lm()* in base R, β-GL(M)Ms, including the occupancy models, were

implemented using the *glmmTMB* package [58]. SEMS were performed using *piecewiseSEM* [59] and effect sizes calculated using *semEff* [60].

Results

Urban density consistently reduced consumer richness of primary consumers and predators (Fig. 2, Table S4). In contrast, local habitat quality increased richness of both primary consumers and predators (Fig. 2). In the joint repeated-measures model, we found no evidence that predator richness declined more strongly than primary consumer richness along the urban density gradient (Fig.S5). Primary consumer richness was higher in larger gardens, but not predator richness (Fig. S4). Allotment gardens had significantly higher predator richness than private gardens (Fig. S4).

Both environmental gradients also influenced trophic composition (Fig. 2). Higher local habitat quality and urban density were associated with shorter food chains (lower mean trophic level, Fig. 2). Both local habitat quality and urban density increased null-standardised degree skewness, indicating a dominance of poorly connected nodes (Fig. 2). This was also the case in private compared to allotment gardens (Fig. S4). Moreover, urban density reduced residual generality, realised consumer diet breadth narrowed beyond expected from changes in taxonomic richness alone. While omnivory did not respond to urban density or local habitat quality, more omnivory was observed in allotment gardens than in private gardens (Fig. S4).

Local habitat quality and urban density both influenced the structural organisation of local webs (Fig. 2). The degree to which observed local webs were more modular than expected (null-standardised modularity) weakened with both higher local habitat quality and urban density. Local webs exhibited higher null-standardised nestedness with increased local habitat quality, but not urban density (Fig. 2).

298 Gardens experiencing higher levels of urban density exhibited faster network fragmentation
299 (faster declines in R_{coef}), but the decline was significantly steeper when nodes were removed
300 according to their sensitivity to urban density, than when removed randomly (Fig. 3A, Table
301 S5). Moreover, private gardens demonstrated lower R_{coef} values than allotment gardens
302 when nodes were removed according to urban sensitivity (Fig. S7). Contrastingly, secondary
303 extinctions only accumulated more rapidly (R_{50} of consumer nodes) along the urban density
304 gradient when removals followed a random order, rather than when taxa were removed
305 according to their sensitivity to urban density (Figs. 3C, S7). There were no significant
306 differences in R_{50} between private and allotment gardens (Fig. S7). Broadly, increased local
307 habitat quality did not maintain robustness according to either metric (Figs. 3B, D, S7),
308 except for a marginal trend to the collapse threshold R_{50} when taxa were removed according
309 to their sensitivity to urban density (Fig. S7).

310 The piecewise SEM demonstrated that urban density led to accelerated network
311 fragmentation (declining R_{coef}) both directly and indirectly through decreases in predator
312 richness and null-standardised nestedness (Fig. 4, see Fig. S9 for random removals).
313 Notably, null-standardised nestedness was associated with lower R_{coef} (Fig. 4a). While null-
314 standardised modularity decreased with increasing urban density, and also indirectly through
315 declines in predator richness, it was not associated with shifts in R_{coef}. However, local habitat
316 quality also decreased modularity directly, though an indirect positive effect through
317 increases in predator richness was also detected (Fig. 4C). While local habitat quality
318 increased predator richness, and led to direct and indirect increases in null-standardised
319 nestedness, these changes did not translate to any total effects on robustness to network
320 fragmentation (Fig. 4C).

321 Urban density led to decreases in mean trophic level, both directly and mediated through
322 changes in predator richness, as well as decreases in residual generality (Fig. 4B). In
323 essence, consumers had access to fewer prey resources than expected, after accounting for
324 the effect of richness in each local web (Fig. 4B,C). Nonetheless, a net positive association

was detected between R_{50} and local habitat quality, indirectly through an increase in null-standardised degree skewness (Fig. 4C). Moreover, local webs where consumers had a higher interaction breadth regardless of local web size (residual generality) were associated with higher R_{50} (Fig. 4B). Both SEMs showed good overall fit to the data (Table S6).

Discussion

Using a multi-trophic metaweb-based approach along urban gardens spanning two largely independent environmental gradients (landscape-scale urban density and local habitat quality), we showed that urban densification systematically restructures food web composition and structure, with consequences for network robustness. Urban density decreased the richness of primary consumers and predators, altered interaction distributions, and increased vulnerability to network fragmentation (R_{coef}) under realistic, sustained extinction scenarios. In contrast, local habitat quality reshaped food webs by increasing predator richness and interaction heterogeneity, resulting in a significant indirect positive effect on the collapse threshold (R_{50}) under sensitivity-based extinction, although this mechanistic effect did not translate into strong differences in realised robustness across gardens.

Urban density and local habitat quality exerted contrasting and partially convergent effects on food-web composition and structure. Urban density, in accordance with other studies, reduced primary consumer and predator richness [13,61]. Urban density can create dispersal challenges and decrease the availability of biotic and abiotic resources, threatening the persistence of insect predators and their prey [12,18]. Consequently, improving local habitat quality promoted the richness of both trophic groups in our gardens. This is in accordance with previous work showing that resource-rich urban green spaces, including flower-rich habitats, can support both herbivorous and predaceous invertebrates [15,62,63]. More broadly, improvements in local habitat quality such as increases in habitat

heterogeneity at the garden scale provide a source of other important ecological resources (i.e. ecological land-use complementation [64]), allowing species across trophic levels to reproduce, survive and contribute to food web functionality [65,66]. Despite these opposing effects on consumer richness, both gradients were associated with decreases in mean trophic level, likely reflecting different processes: trophic truncation driven by the loss of higher trophic taxa under urban density, and a disproportionate expansion of lower relative to higher trophic levels under increased local habitat quality (which included plant richness). Likely due to trophic downgrading [67] and connectivity constraints [68] in highly isolated and fragmented systems, the expansion of resource taxa was not matched by proportional increases in higher trophic levels. Despite local dietary resource availability, invertebrate taxa have been observed to decrease in abundance with urbanisation [15,69], but see [47]. Dispersal—rather than dietary resource—limitation may reduce the ability of less mobile invertebrates to persist within the dense urban matrix [70]. From a metacommunity perspective, increasing isolation among patches may weaken dispersal-mediated rescue and recolonisation, so that locally suitable gardens are less able to maintain species whose persistence depends on exchange among patches [71]. Thus, maintaining connectivity among urban green spaces is necessary alongside local habitat improvements to sustain invertebrate communities [72]. In our gardens, increased urban density was related to a loss in habitat quantity, quality, and connectivity. Maintaining sufficient habitat may be particularly important for predators and parasitoids, which can be disproportionately vulnerable to losses in habitat quantity and connectivity [73,74]. Where habitat quantity cannot be retained, improving connectivity among remaining green spaces may nonetheless partially help mitigate food-web simplification by supporting dispersal and persistence of invertebrates [13].

Shifts in the composition and structure of food webs translated into distinct consequences for the two dimensions of robustness. The contrasting responses of R_{coef} and R_{50} indicate that structural collapse of food webs can occur without accelerated secondary species loss [75].

Urban-sensitive taxa may be disproportionately important for maintaining energy flow among otherwise distinct parts of the food web. Thus, their loss disrupts potential pathways of energy and material flow even while much of the community persists. Robustness assessments based only on collapse thresholds may overlook important structural degradation.

R_{coef} declined strongly with urban density, both directly and indirectly through shifts in predator richness and nestedness. Predators have been documented to increase food web connectance [13] and function as connector taxa, linking otherwise weakly connected prey groups through broad feeding interactions and apparent competition [76,77]. In our system, food web nestedness increased with local habitat quality, yet food webs with higher than expected nestedness were associated with lower R_{coef}. While nestedness has been demonstrated to support stability in pollination and herbivory networks [51,78], its stabilising role has increasingly been questioned, particularly when accounting for competition among consumers for shared resources [79]. This may be particularly relevant in cities, where urbanisation can disproportionately remove scarce, weakly connected taxa, leaving remnant food webs still highly connected [21]. Theoretical and empirical work supports this line of thought, showing that multi-trophic networks can become vulnerable when interactions are concentrated around a small number of highly connected taxa, increasing dependence on shared resources and vulnerability to their loss [80–82].

While modularity decreased with urban density beyond the effects due to richness, it was not associated with robustness to fragmentation. This may be as our multi-trophic food webs are dominated by generalists, and generally not extremely modular. Therefore, it is understandable that robustness to fragmentation in our networks was not mediated by modularity, but through predator richness. Theory suggests that food web stability can be enhanced in more weakly-connected architectures rather than highly nested ones [50], consistent with our finding that higher than expected degree skewness was associated with higher R_{50}. Although R_{50} responded to extinction order, it did not decline with urban density

itself. Instead, local habitat quality indirectly increased R_{50} through higher degree skewness and lower mean trophic level, potentially promoting a more diffuse, pyramid-like network structure [16,83]. However, these local improvements did not increase R_{coef}, indicating that greater resistance to secondary extinctions did not necessarily increase the structural cohesion of the food web. In urban gardens, these effects may be fostered by management that increases plant and structural diversity, retains detrital resources and water, and reduces disturbance regime, thereby broadening resources and refugia for primary consumers. Restoring the connected backbone of the food web, particularly through higher trophic levels, may require additional landscape-scale measures that maintain sufficient habitat amount and connectivity, especially for actively dispersing species.

Limitations and perspectives

We assessed whether local habitat improvements could buffer the effects of urban densification on local community and food web structure. By reducing multiple habitat attributes to a single PCA axis and grouping species into broad consumer groups (e.g., predators), we assume broadly comparable taxon-level responses despite habitat requirements being species-specific. The derived network responses should therefore be interpreted as community-level tendencies, since disproportionate changes within trophic levels may not be captured by a single habitat-quality gradient. Nonetheless, the positive association between local habitat quality and primary consumer and predator richness indicates that broad habitat improvements can still capture meaningful community-level responses. More generally, while SEM proved valuable here, future studies should explore non-linear extensions to better capture the complexity of urbanisation effects on food-web structure.

We inferred local webs from co-occurring taxa using a regional metaweb of documented interactions, rather than from directly observed interactions. This approach has been criticised to lack ecological realism [84]. Yet, in the absence of observed interaction data, the

metaweb approach provides a standardised way to compare changes in network structure arising from community turnover [13,38,55]. Accordingly, mean trophic level should be interpreted as a local-web metric rather than a fixed species-level trait, reflecting both the compositional loss of high-trophic-level taxa and changes in the realised trophic positions of taxa retained in local webs. The concurrent decline in predator richness, classified independently using the metaweb, suggests that predator loss contributed to this pattern, but the two mechanisms cannot be fully separated without observed interaction data. Although there have been repeated calls for more empirical investigations into multi-trophic food web structure in urban systems [1,85], logistical and methodological constraints have largely limited urban interaction sampling to bipartite networks [11,15,86].

Our extinction simulations used unweighted food webs and therefore focused primarily on bottom-up consequences of species loss. Yet, top-down effects and variation in interaction strengths can also influence food web stability [87]. Moreover, changes in species abundances may alter encounter rates and realised diets without species loss, while anthropogenic subsidies may create feeding links not represented in the metaweb [1]. Future studies should aim to combine abundance and interaction data to construct weighted networks, evaluate both top-down and bottom-up extinction dynamics, and link interaction structure to measured ecosystem functions [88]. Given the growing potential to incorporate food webs into systematic conservation planning [19], expanding empirical interaction datasets in urban systems is certainly worth prioritising. Meanwhile, the use of metaweb-based approaches remains one of the few alternatives to study urban food webs.

Conclusions

We demonstrate that urban densification is likely to produce trophically simplified food webs with fewer primary consumers and predators and decreased structural robustness to species loss. Increased local habitat quality partially compensated for predator loss and indirectly increased resistance to secondary extinctions, but did not restore structural robustness.

Even though local improvements can enhance key ecosystem functions and underlying services such as pest control [28], pollination [15] and decomposition [47], maintaining biodiversity in urban systems will require landscape-scale measures that retain and restore green-space habitat, improve connectivity among patches, and use small-scale urban greening interventions to reduce isolation [20]. Urban densification is increasingly implemented to prevent urban sprawl and curb net land loss [7], but cannot proceed on the assumption that compactness is biodiversity-neutral. Safeguarding urban biodiversity and ecosystem functions will also require connected, high-quality green infrastructure [20] that sustains robust food webs, and maintains the valuable contributions of urban biodiversity to the multitudes who call cities home.

Conflict of interest

We declare that we have no conflicts of interest.

Author contributions

MR, KP and MM conceptualised the study. MR, KP, JCA, BF, DJF and MM designed methodology. MM, JCA, BF, DJF and GC collected data. MR and BF curated data. MR conducted the formal analysis and wrote the initial draft. All authors commented on and approved the final draft.

Data accessibility

All data are publicly available and cited in the methodology; analysis data and code are available upon publication.

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489

Figures

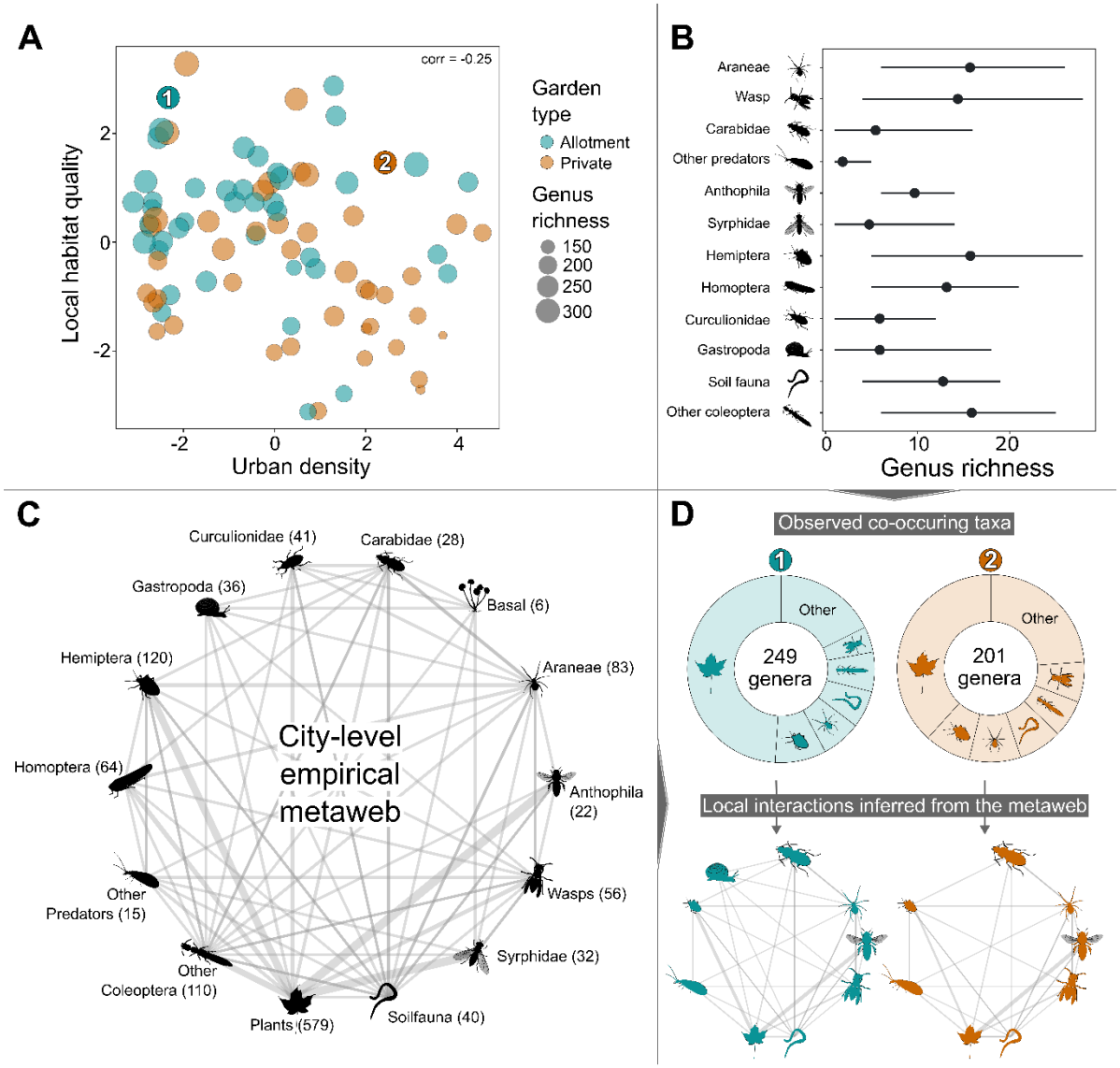


Figure 1. (A) Study sites plotted along two gradients: urban densification and local habitat quality. Point size represents genus richness, colours represent garden type (orange: private, teal: allotment). (B) Taxa-specific genus richness. Points represent mean value, bars represent standard deviation. (C) City-level metaweb. Link thickness represents the number of interactions between taxa in those large groups, numbers in parentheses refer to total taxonomic richness of each group. (D) Co-occurrences in each site are combined with interactions documented in the metaweb to infer local garden level food webs. Two examples are shown, representing the study sites marked 1 and 2 in (A).

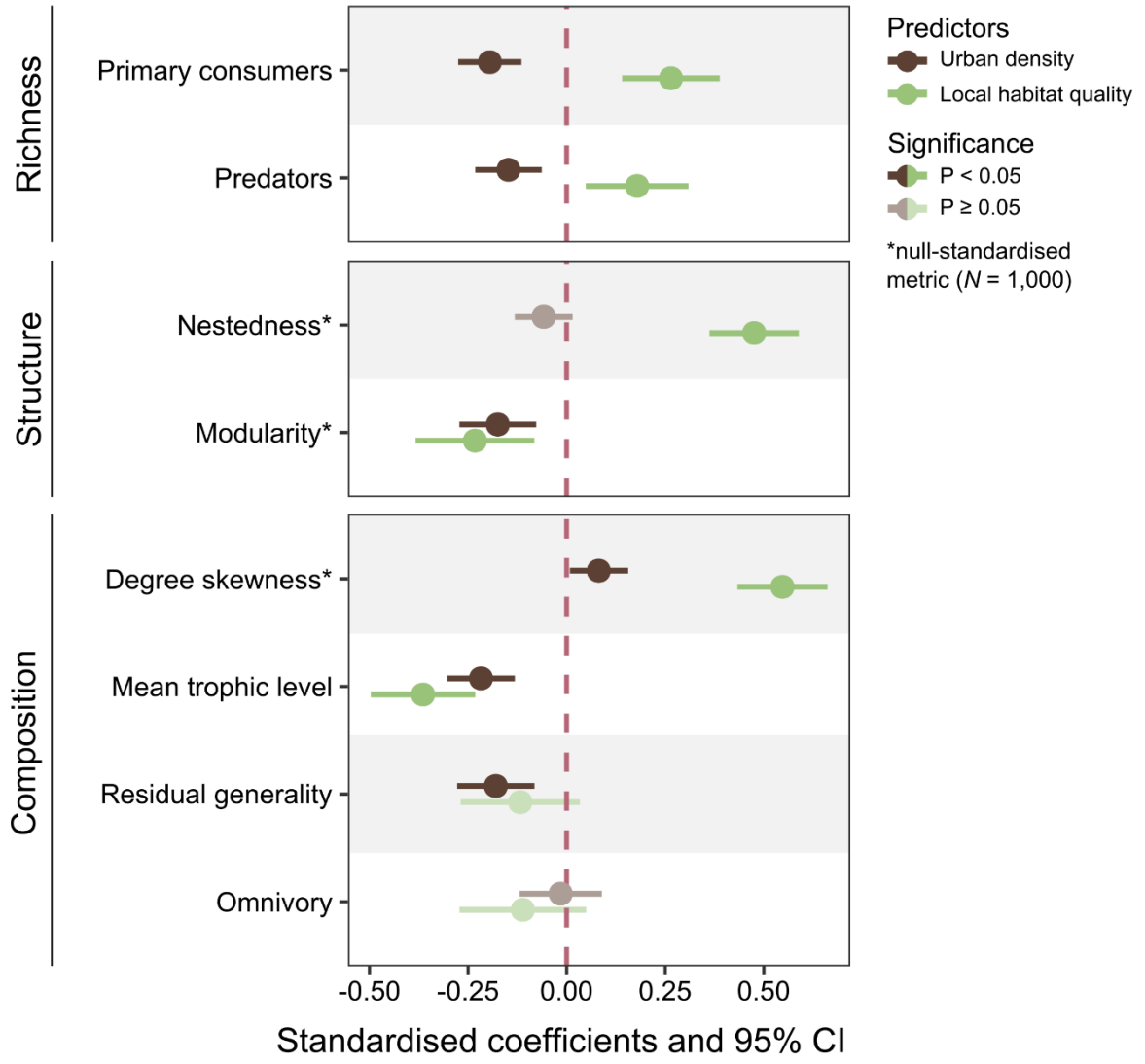
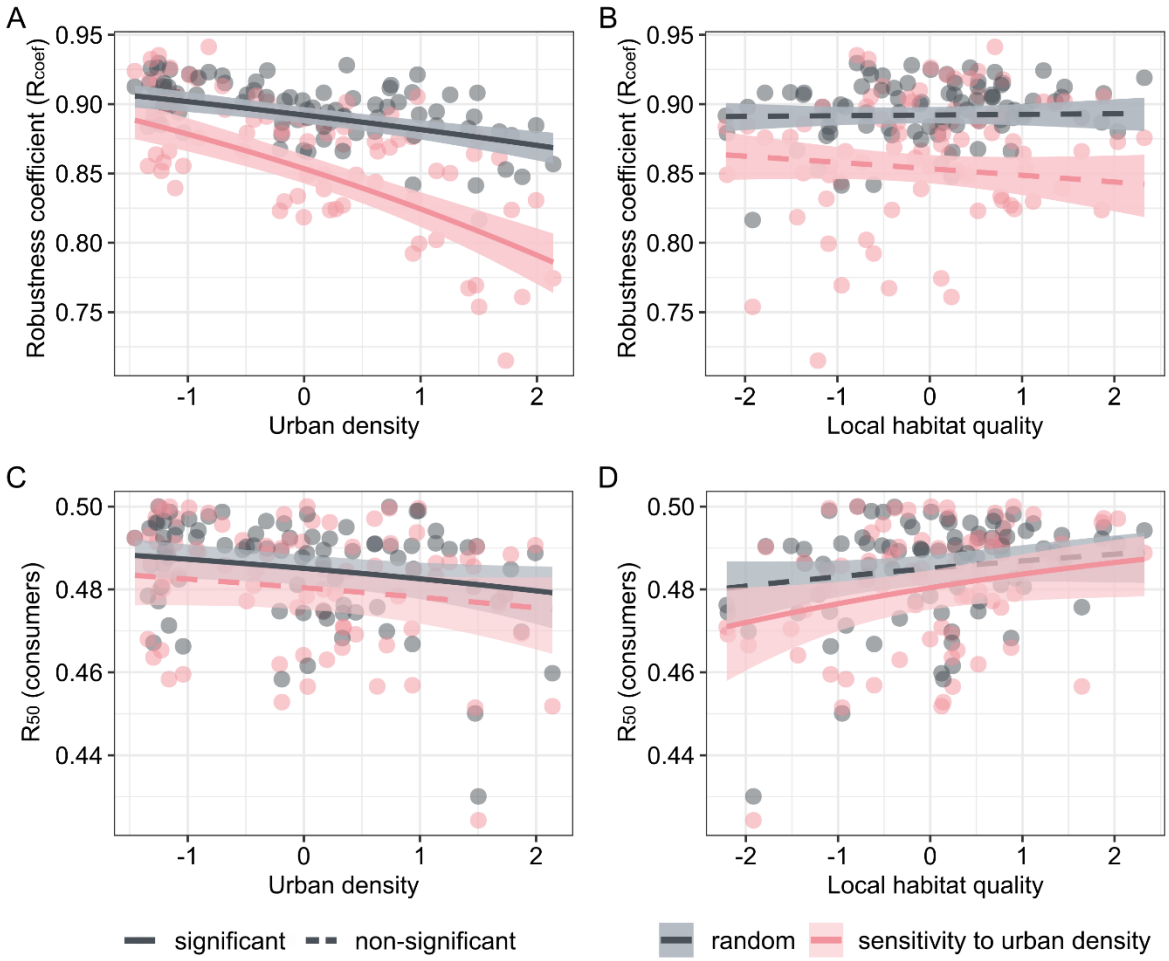


Figure 2. **Responses of local webs to local habitat quality and urban density.** Standardised coefficients (±95% CI) from linear models relating richness-based, compositional and structural metrics to local habitat quality (green) and urban density (brown). * indicates usage of a z-score rather than the raw network metric to control for differences in network size and link density. Points indicate model estimates; coloured symbols show significant effects (P < 0.05), transparent symbols indicate non-significant effects.



508

509 *Figure 3.* **Effects of urban density and local habitat quality on local food-web**
510 **robustness under random vs. urban-sensitivity extinction scenarios**. (A-B) Partial
511 effects of urban density and local habitat quality on robustness coefficient (R_{coef}). (C-D)
512 Partial effects of urban density and local habitat quality on R_{50} of consumers. Predicted
513 relationships (lines ±95% CI ribbons) presented for random (grey) and urban sensitivity-
514 based (pink) extinctions. Dashed lines represent non-significant predictors. Points represent
515 mean values from 1,000 replicates per garden.

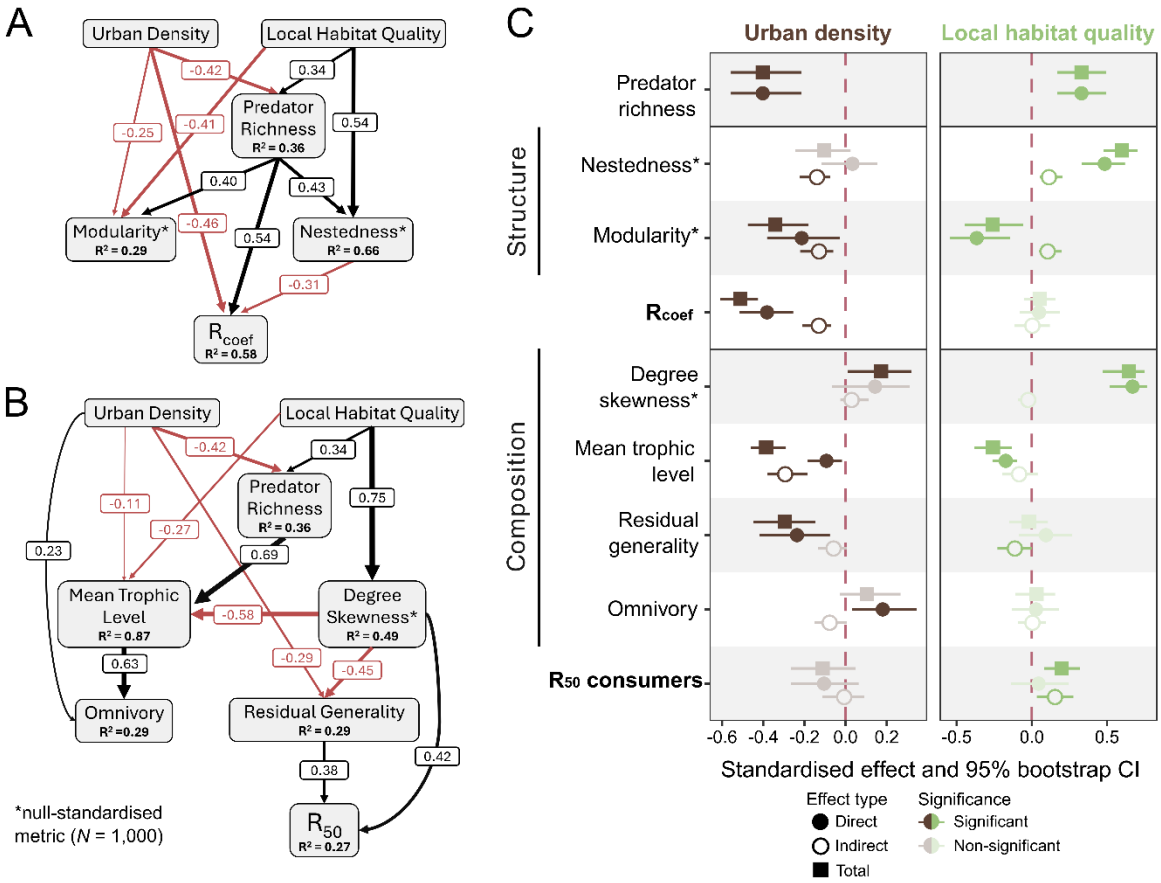


Figure 4. **Structural equation models linking urban density and local habitat quality with structural and compositional properties of local food webs and robustness against the removal of taxa sensitive to urban density.** Black arrows indicate positive effects, red arrows indicate negative effects ($P < 0.05$). Only significant relationships are presented. (A) Standardised path coefficients (|β| shown on arrows) describe direct relationships among predictors and compositional food-web metrics: degree skewness (z-score relative to null models), mean trophic level, residual generality (independent of richness), omnivory, and R_{50} threshold (consumers only). (B) Standardised path coefficients (|β| shown on arrows) describe direct relationships among predictors, predator richness, structural metrics: nestedness, modularity (all expressed as z-scores relative to null models) and robustness coefficient R_{coef}. (C) Total, direct and indirect effects of urban density and local habitat quality on local web composition, structure, and robustness. Shapes indicate effect types (filled round for direct, open round for indirect, square for total), with lines representing 95% confidence intervals derived from bootstrapped standardised coefficients (10,000 resamples). Transparent points represent non-significant relationships.

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Urban densification reduces food-web robustness despite partial gains through local habitat improvements

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Supporting Information

Methods: Biodiversity sampling

Vascular plant occurrences were acquired through a floristic inventory of entire garden lots based on repeated visits to the gardens across the entire growing season in 2015, and supplemented with vegetation relevés on two standardised plots (10 m^2) per garden in the summer of 2015 (Frey & Moretti, 2019). Surface-dwelling arthropods were sampled in each garden using six 70-mm diameter pitfall traps. The traps were covered with transparent plastic roofs for rain protection and placed in two habitat types, one uncultivated (e.g. lawns, meadows) and one cultivated (e.g. flower or vegetable beds). Flying insects were sampled with coloured 1-litre pan-traps and placed in a central, unshaded position in each garden (e.g. on the lawn or meadow). Both pitfall and pan traps were continuously open between May and August 2015 and emptied on a weekly basis. Further details are available (Casanelles-Abella et al., 2026). Parasitoids and kleptoparasites were sampled using trap nests (Martínez-Núñez et al., 2024). We fixed three empty trap nests per garden in February 2016 and collected the trap nests in October 2016. We subsequently opened all brood cells and identified the natural enemies. Further details are available (Martínez-Núñez et al., 2024).

Invertebrates were stored in 70%, sorted in the laboratory and sent to experts for identification. While most were identified to the species level, when this was not possible, the identification was kept to the genus level. In total we sampled 578 vascular plants, 22 bees, 83 spiders, 28 carabid beetles, 41 weevils, 109 other beetles, 36 gastropods, 120 hemipterans, 63 homopterans, 1 scorpionfly, 13 neuropterans, 32 hoverflies, 55 wasps, 13 isopods and 17 myriapods at the genus level.

Methods: Metaweb

The city-level metaweb was primarily built using the existing Swiss-level metaweb, which was constructed using trophic interactions sourced from the literature, including empirical natural history observations, extensive quantitative field research and voluntary science (Reji Chacko, Albouy, Altermatt, Casanelles-Abella, et al., 2025). However, some groups (e.g. horticultural plants) were not well-represented by this dataset, which focused on species present within the national vascular plant checklist, which excludes non-native plants like horticultural taxa (Reji Chacko, Albouy, Altermatt, Casanelles-Abella, et al., 2025). Thus, we sourced additional trophic interactions from the literature to complete the metaweb (Table S1). We collapsed the metaweb to the genus-level resolution, as it has been demonstrated to sufficiently capture changes in trophic dynamics across various environmental gradients (Potapov et al., 2019; Thompson & Townsend, 2000). It also allowed us to minimise biases towards taxa with well-documented interactions, without having to exclude groups where diets were often not well-documented at the species resolution (e.g. generalist predators or soil fauna). As some primary consumers were still all-together lacking in genus-level resources, we included their resources within feeding guilds. These included categories such as e.g. detritus, moss, algae, bark, microbes, and others as defined in the Swiss metaweb (Reji Chacko, Albouy, Altermatt, Casanelles-Abella, et al., 2025). We assumed these large resource pools to be always available, in line with other metaweb-based approaches (Perrelet et al., 2025; Reji Chacko, Albouy, Altermatt, Boussange, et al., 2025). Admittedly, this is an oversimplification, particularly for urban ecosystems where such resources are

more likely to be missing, and other anthropogenic subsidies are likely to be present. Nonetheless, this approach was also necessary in order to correctly classify primary consumers feeding on basal resources outside of vascular plants. The network-based classification would have misclassified them as basal resources themselves, as they would otherwise have a trophic level of 1. The final metaweb consisted of 17,314 interactions between 1,210 genera and 22 feeding guilds.

We inferred local garden-level food webs (henceforth: local web) through a co-occurrence based approach (Ho et al., 2022; Neff et al., 2021; Reji Chacko, Albouy, Altermatt, Boussange, et al., 2025). To do this, we assumed that if taxa co-occurred in a garden according to our sampling, their interactions would be inherited directly from the regional metaweb. To generate baseline expectations for network structure, we also built constrained null models for each local web. For every garden, we retained the observed number of taxa and trophic links, but replaced the actual interactions with randomly drawn consumer–resource pairs. Allowed links were defined as all possible directed edges between any consumer and any potential resource within that garden's species set, excluding cannibalistic interactions. Primary resources were first classified as those which have a trophic level of 1 in the metaweb. Such taxa were not allowed to act as consumers, ensuring that null webs respected the empirical trophic role partitioning while remaining otherwise interaction-neutral. For each garden, interactions were sampled without replacement from this allowed set to assemble one null network, and this procedure was repeated 1,000 times to generate a distribution of null webs. Each resulting randomised web was then subjected to the same metric calculations as the empirical webs. This approach isolates the contribution of basic network size and trophic role composition, while removing most biologically structured interaction patterns, thereby providing a reference against which empirical structure can be evaluated. Local webs were significantly different from null model expectations (Figure S3).

Methods: Sensitivity of richness models to error distribution.

Primary consumer and predator richness were modelled using Gaussian errors in the main analyses to maintain a consistent modelling framework across food-web metrics. Richness values were relatively large (range = 18–63 genera; mean = 42.8), and Gaussian model residuals showed no substantial departures from normality or homoscedasticity. As a sensitivity analysis, richness models were refitted using Poisson and negative-binomial error distributions (Table S7). The direction and interpretation of effects of urban density, local habitat quality and garden type were consistent across distributions. Garden area was positively associated with richness in all models, although statistical support was stronger under the Poisson and negative-binomial models than under the Gaussian model. We therefore retained the Gaussian models for the main analyses.

Methods: Sensitivity of SEMs to garden-level covariates

We assessed whether inclusion of garden area and garden type affected inference regarding the two focal environmental gradients. Log-transformed garden area was not associated with either urban density ($r = -0.08$, $p = 0.445$) or local habitat quality ($r = 0.06$, $p = 0.583$). Garden type was associated with both gradients, although it explained relatively little variation in urban density ($R^2 = 0.06$) and local habitat quality ($R^2 = 0.10$). We therefore compared the final parsimonious SEMs, containing only the hypothesised environmental and food-web pathways, with otherwise identical models additionally including garden area and garden type as covariates in all component models. Direct component-path estimates and bootstrapped direct, indirect and total effects of urban density and local habitat quality were qualitatively similar between model specifications (Fig. S10). We therefore retained the parsimonious SEMs for the main analysis.

Methods: Urban-sensitivity scenario: estimating removal probabilities

The sensitivity of a genus to densification was quantified using a mixed-effects occupancy model based on presence–absence data across all gardens. Species occurrences were

aggregated at the genus level to match the resolution of the network analyses. For each genus, presence in a garden was modelled as a function of urban density, local habitat quality, garden area, and garden type using a binomial GLMM. To allow taxa to differ in their responses to densification, we included genus-specific random intercepts and random slopes for urban density. This structure captured both baseline differences in occupancy and heterogeneity in urban-sensitivity among taxa.

We extracted genus-level sensitivity values as the random-slope-adjusted coefficient for urban density ($\beta_{density}$), calculated as the sum of the fixed effect of densification and each genus's random slope deviation. More negative $\beta_{density}$ values indicate genera whose occupancy declines steeply with increasing urban density (i.e., high urban-sensitivity). These sensitivity estimates were then used to weight extinction probabilities in the robustness simulations, allowing extinction sequences to reflect environmentally structured species loss.

In the second robustness scenario, removal probability was proportional to $\exp(-k \cdot \beta)$, with β representing the taxon's estimated sensitivity to urban density (using the estimated β coefficients from occupancy models) and k controlling how strongly these differences among these coefficients affected removal probabilities. This probabilistic weighting ensured that strongly contrasting taxa were generally removed in the expected order, but taxa with similar estimated sensitivities could vary in their order of removal among simulations.

To evaluate whether our results depended on the strength of the sensitivity-weighted extinction bias, we repeated the robustness analysis across five values of k, spanning weakly stochastic to nearly deterministic removal sequences. For each k, we fitted β-GLMMs testing the effects of urban density, local habitat quality, garden type, and garden area on two robustness metrics. Across all k values, model coefficients were consistent in both magnitude and direction, and the significance patterns of predictors were effectively unchanged (Fig. S2). We thus selected the most intermediate k-values for all further analyses.

142 *Table S1.* Metrics used to build the urban density predictor. All metrics (except those
143 pertaining to distances) were calculated at the landscape-scale in a 500-m buffer around the
144 garden site.

145

Dimension	**Metric**	**Dataset**
Quantity	Proportion of impervious surface	Copernicus Impervious Density 2015. 20-m resolution (Copernicus Land Monitoring Service, 2018b)
	Change in the proportion of impervious surface	Difference between Copernicus Impervious Density 2015 and 2006. 20-m resolution(Copernicus Land Monitoring Service, 2018a, 2018b)
	Average building height	LIDAR data from 2014 (see data availability statement)
Connectivity	Green Patch Cohesion Index	Habitat Map of Zurich. 1-m resolution. (Grün Stadt Zürich, 2022)
	Distance to the nearest body of water	
	Distance to nearest forest	
Quality	The number of habitats mapped in the buffer around the garden, from a total of 62 habitat types.	
	The standard deviation of vegetation height	LIDAR data from 2014 (see data availability statement)
	Proportion of high NDVI sites	Structural vegetation topology map (Casciano et al., In revision)

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147 *Table S2* List of all resources with interactions. For a per-interaction citation, please
148 download the associated data from https://doi.org/10.16904/envidat.795
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151 *Table S3 Glossary of network-related terms and their calculation.*

Term	**Definition and method of calculation**
Basal resource	Primary producers such as plants as well as taxonomically low-resolution nodes in the food web which never behave as consumers (trophic level = 1)
Generality	The mean number of resources per consumer in the food web (Schoener, 1989). As this measure increases with total richness, we used richness-corrected generality, calculated as the residuals from a linear model relating generality to taxonomic richness per local web.
Largest Weakly Connected Component (LWCC)	LWCC represents the largest of the sub-networks in each food web. The size of the LWCC was calculated by first identifying the LWCC from the list of WCC using *components()* in the R package *igraph* (Csárdi et al., 2024) and then taking the sum of nodes in that component.
Link	A trophic interaction between two nodes (Dunne, 2006).
Mean trophic level	The average position of a node in a food web, based on their feeding relationships (Williams & Martinez, 2004). Mean trophic level was calculated as the mean prey-averaged trophic level of all taxa within each food web using the *PreyAveragedTrophicLevel()* function in the R package *cheddar* (Hudson et al., 2013).
Modularity	The extent to which interactions in the food web are grouped into relatively exclusive clusters (Blüthgen & Staab, 2024). Modularity was calculated using the walktrap community detection algorithm implemented in *igraph* (Csárdi et al., 2024). For each directed food web, communities were identified with *cluster_walktrap()*, and modularity was then extracted from the resulting community structure using *modularity()*.
Nestedness	The extent to which interactions in the food web by specialised species are a subset of interactions by generalist species, as opposed to being exclusive interactions (Blüthgen & Staab, 2024). Nestedness was quantified based on Overlap and Decreasing Fill (NODF), using the *nestednodf()* function in the R package *vegan* (Oksanen et al., 2020).
Node	Individual taxon or resource (e.g. algae) within the food web (Dunne, 2006).
Node degree skewness	The degree to which the distribution of links in a food web is skewed. A positive skew relates to a dominance of nodes with few links, and a negative skew relates to a dominance of nodes with

	many links (Dunne et al., 2002). We calculated using *skewness()* function in the R package *e1071* (Meyer et al., 2025).
Omnivory	The degree to which consumers feed on resources in multiple trophic levels. Omnivory was quantified as the mean standard deviation of prey trophic levels across consumers within each food web, following calculations based on the *PreyAveragedTrophicLevel()* function in the R package *cheddar* (Hudson et al., 2013).
Predator richness	Total number of higher order consumers, taxa which feed on at least on a resource which has a trophic level of 2 or higher, based on the position in the metaweb, per local web.
Primary consumer richness	Total number of primary consumers, taxa which are exclusively feeding on basal resources (trophic level = 2), based on the position in the metaweb, per local web.
R_{50}	The proportion of nodes that must be removed before 50% of the nodes in the food web have become extinct (Keyes et al., 2024).
Robustness coefficient (R_{coef})	The area under the extinction curve of the LWCC, divided by the maximum possible area under a linear decline from the initial LWCC size until all nodes are fully removed. Values closer to 1 indicate that the food web retained a large connected component for longer, and fewer secondary extinction, during sequential extinction, whereas values closer to 0 indicate rapid network collapse (Piraveenan et al., 2013).
Weakly Connected Components (WCC)	WCCs represent isolated sub-networks in each food web. The number of WCC were calculated using the *components()* function in the R package *igraph (Csárdi et al., 2024)*

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Table S4. Standardised coefficients from linear models testing the effects of local habitat quality, urban density, garden area and garden type on trophic richness, food-web composition and network structure. Estimates are shown with 95% confidence intervals. Garden area was log-transformed and standardised prior to analysis; garden type represents private gardens relative to allotment gardens. Adjusted R^2 values are given in parentheses for each response model. Nestedness, modularity and degree skewness (*) were expressed as z-scores relative to 1,000 constrained null-model networks. Significant effects were assessed at $P < 0.05$.

Response (Adj. R^2)	Predictor	Estimate [95% CI]	t	*P*
Primary consumers (0.44)	Local habitat quality	0.26 [0.14, 0.39]	4.19	<0.001
	Urban density	-0.19 [-0.27, -0.11]	-4.76	<0.001
	Garden area	0.23 [0.06, 0.41]	2.56	0.012
	Garden type (private)	0.06 [-0.32, 0.44]	0.29	0.769
Predators (0.38)	Local habitat quality	0.18 [0.05, 0.31]	2.69	0.009
	Urban density	-0.15 [-0.23, -0.06]	-3.43	<0.001
	Garden area	0.17 [-0.02, 0.36]	1.75	0.084
	Garden type (private)	-0.64 [-1.04, -0.24]	-3.12	0.002
Degree skewness* (0.52)	Local habitat quality	0.55 [0.43, 0.66]	9.39	<0.001
	Urban density	0.08 [0.01, 0.15]	2.11	0.038
	Garden area	0.08 [-0.08, 0.25]	0.96	0.338
	Garden type (private)	0.45 [0.09, 0.80]	2.49	0.015
Mean trophic level (0.36)	Local habitat quality	-0.36 [-0.50, -0.23]	-5.39	<0.001
	Urban density	-0.22 [-0.30, -0.13]	-4.96	<0.001
	Garden area	0.11 [-0.09, 0.30]	1.07	0.287
	Garden type (private)	-0.50 [-0.91, -0.09]	-2.41	0.018
Residual generality (0.17)	Local habitat quality	-0.12 [-0.27, 0.03]	-1.53	0.131
	Urban density	-0.18 [-0.28, -0.08]	-3.60	<0.001
	Garden area	0.06 [-0.16, 0.27]	0.50	0.620
	Garden type (private)	-0.45 [-0.91, 0.02]	-1.90	0.062
Omnivory (0.06)	Local habitat quality	-0.11 [-0.27, 0.05]	-1.36	0.179
	Urban density	-0.02 [-0.12, 0.09]	-0.28	0.777
	Garden area	-0.03 [-0.27, 0.20]	-0.28	0.783
	Garden type (private)	-0.62 [-1.11, -0.13]	-2.46	0.016
Nestedness* (0.53)	Local habitat quality	0.48 [0.36, 0.59]	8.24	<0.001

Response (Adj. R^2)	Predictor	Estimate [95% CI]	t	*P*
	Urban density	-0.06 [-0.13, 0.02]	-1.56	0.123
	Garden area	0.12 [-0.04, 0.29]	1.49	0.141
	Garden type (private)	-0.08 [-0.42, 0.27]	-0.43	0.671
Modularity* (0.17)	Local habitat quality	-0.23 [-0.38, -0.08]	-3.03	0.003
	Urban density	-0.17 [-0.27, -0.08]	-3.51	<0.001
	Garden area	0.08 [-0.14, 0.30]	0.72	0.471
	Garden type (private)	-0.38 [-0.85, 0.08]	-1.63	0.107

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Table S5. Fixed-effect estimates from beta regression models testing the effects of urban density, local habitat quality, garden type, garden area, and the interaction between urban density and local habitat quality on two complementary measures of food-web robustness: the robustness coefficient (R_{coef}) and the collapse threshold (R_{50}). Models were fitted separately for random and urban-sensitivity extinction scenarios. Estimates are presented on the model link scale with 95% confidence intervals. Garden area was log-transformed prior to analysis, and garden type represents private gardens relative to allotment gardens. For R_{50}, values were rescaled prior to beta regression as described in the Methods. P-values are based on Wald z-tests.

Metric	Scenario	Predictor	Estimate [95% CI]	z	*P*
R_{coef}	Random	Urban density	-0.10 [-0.15, -0.06]	-4.90	<0.001
		Local habitat quality	0.00 [-0.04, 0.05]	0.10	0.917
		Garden type (private)	-0.08 [-0.18, 0.01]	-1.77	0.076
		Garden area	0.04 [-0.01, 0.08]	1.64	0.100
		Urban density × Local habitat quality	-0.01 [-0.05, 0.04]	-0.35	0.725
	Urban sensitivity	Urban density	-0.21 [-0.27, -0.16]	-7.40	<0.001
		Local habitat quality	-0.04 [-0.10, 0.02]	-1.35	0.179
		Garden type (private)	-0.28 [-0.41, -0.15]	-4.25	<0.001
		Garden area	0.05 [-0.01, 0.11]	1.58	0.114
		Urban density × Local habitat quality	0.02 [-0.04, 0.08]	0.70	0.483
R_{50}	Random	Urban density	-0.15 [-0.30, -0.00]	-1.98	0.048
		Local habitat quality	0.12 [-0.04, 0.28]	1.42	0.157
		Garden type (private)	-0.02 [-0.35, 0.31]	-0.11	0.913
		Garden area	0.06 [-0.09, 0.22]	0.79	0.427
		Urban density × Local habitat quality	-0.03 [-0.20, 0.14]	-0.35	0.725
	Urban sensitivity	Urban density	-0.11 [-0.26, 0.04]	-1.39	0.164
		Local habitat quality	0.17 [-0.00, 0.34]	1.96	0.050
		Garden type (private)	-0.16 [-0.51, 0.19]	-0.91	0.361

		Garden area	0.11 [-0.05, 0.28]	1.34	0.182
		Urban density × Local habitat quality	-0.05 [-0.23, 0.12]	-0.61	0.542

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Table S6. Overall fit of the structural and compositional piecewise structural equation models (SEMs). Model fit was assessed using Fisher's C statistic; non-significant P-values indicate no evidence of overall model misfit.

SEM	**Fisher's C**	**df**	**P**
Structural (R_{coef})	1.163	2	0.559
Composition (R_{50})	5.392	2	0.067

Table S7. Sensitivity of primary consumer and predator richness models to alternative error distributions. Coefficient magnitudes are not directly comparable among model families because they are expressed on different scales; comparisons are intended to assess consistency in the direction and statistical support of predictor effects.

Response	Predictor	Distribution	Estimate [95% CI]	P
Primary consumers	Local habitat quality	Gaussian	0.265 [0.141, 0.388]	<0.001
		Poisson	0.053 [0.033, 0.072]	<0.001
		Negative binomial	0.052 [0.028, 0.076]	<0.001
	Urban density	Gaussian	-0.195 [-0.275, -0.114]	<0.001
		Poisson	-0.039 [-0.052, -0.026]	<0.001
		Negative binomial	-0.039 [-0.054, -0.024]	<0.001
	Garden area	Gaussian	0.235 [0.055, 0.414]	0.012
		Poisson	0.049 [0.020, 0.078]	<0.001
		Negative binomial	0.050 [0.015, 0.084]	0.005
	Garden type (private)	Gaussian	0.057 [-0.324, 0.438]	0.769
		Poisson	0.005 [-0.055, 0.065]	0.874
		Negative binomial	0.002 [-0.071, 0.074]	0.966
Predators	Local habitat quality	Gaussian	0.179 [0.048, 0.309]	0.009
		Poisson	0.041 [0.016, 0.067]	0.002
		Negative binomial	0.041 [0.013, 0.070]	0.005
	Urban density	Gaussian	-0.148 [-0.232, -0.063]	<0.001
		Poisson	-0.034 [-0.050, -0.017]	<0.001
		Negative binomial	-0.034 [-0.053, -0.016]	<0.001

	Garden area	Gaussian	0.169 [-0.020, 0.358]	0.084
		Poisson	0.042 [0.005, 0.079]	0.026
		Negative binomial	0.043 [0.001, 0.084]	0.044
	Garden type (private)	Gaussian	-0.639 [-1.040, -0.238]	0.002
		Poisson	-0.147 [-0.225, -0.069]	<0.001
		Negative binomial	-0.148 [-0.235, -0.060]	<0.001

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Figure S1. **Principal component analyses used to derive the two environmental predictor gradients.** (A) PCA of landscape-scale urban density variables measured within a 500-m buffer around each garden, summarising habitat quantity, quality and connectivity. PC1 explained 50.7% of the variance and represents the urban density gradient used in the analyses. (B) PCA of local habitat variables, including management intensity, structural diversity, plant diversity, proportion of detritus and water availability. PC1 explains 40.1% of the variance and represents the local habitat quality gradient. Points show individual gardens; arrows indicate variable loadings.

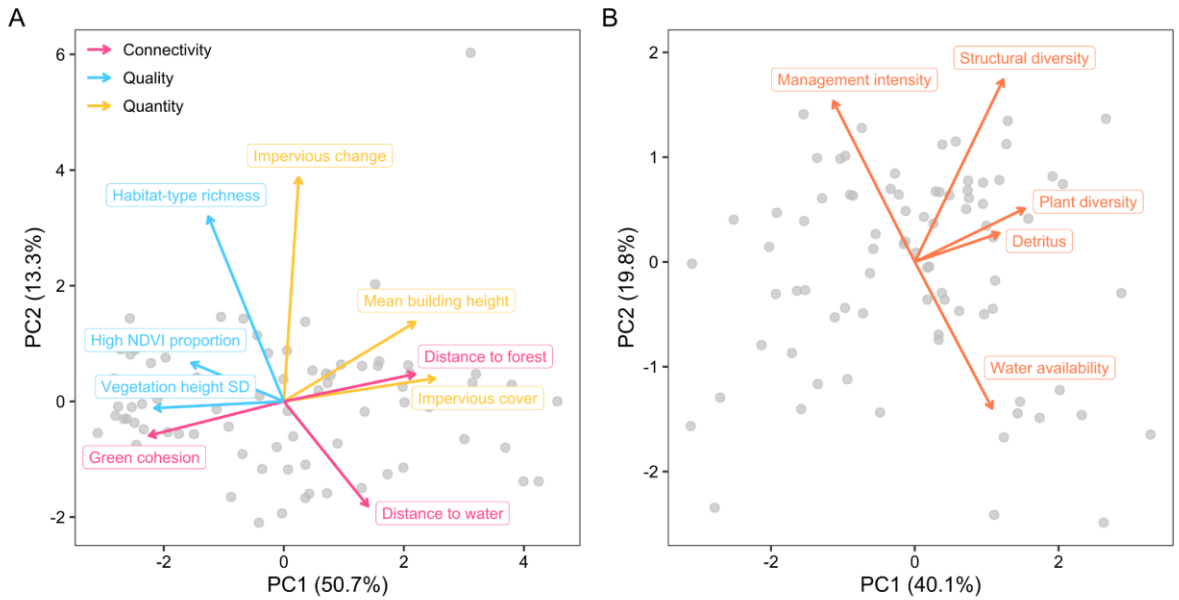


Figure S2. **Sensitivity analysis across alternative values of the extinction-bias parameter k.** Standardised coefficient estimates (±95% CI) from β-GLMMs testing the effects of urban density, local habitat quality, garden type, and garden area on the two robustness metrics, R_{coef} and R_{50}, across five values of the sensitivity parameter *k* (colours). In the urban-sensitivity extinction scenario, *k* controls the strength of the bias in extinction probability towards taxa that are more sensitive to urban density, ranging from weakly stochastic to near-deterministic extinction sequences.

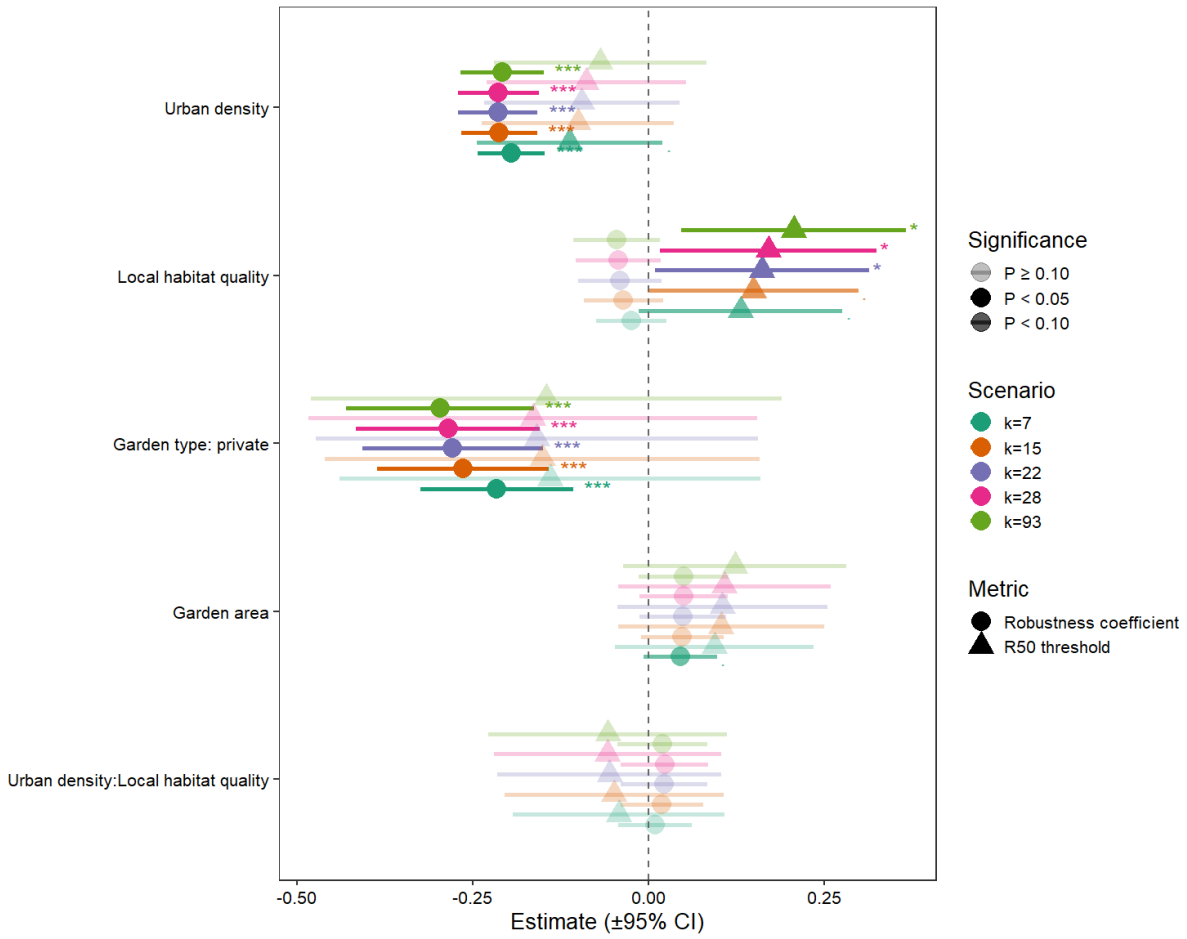


Figure S3. **Comparison of empirical garden food webs with constrained null-model webs.** (A) PCA of empirical and randomised food webs based on five network metrics: nestedness, modularity, degree skewness, mean trophic level and omnivory. Points represent individual empirical webs or means of 1,000 null-model replicates; ellipses show group-level clustering. (B) The distribution of empirical values relative to null-model distributions. (C) Observed minus null mean values for each garden. Orange vertical lines indicate zero difference from null expectations.

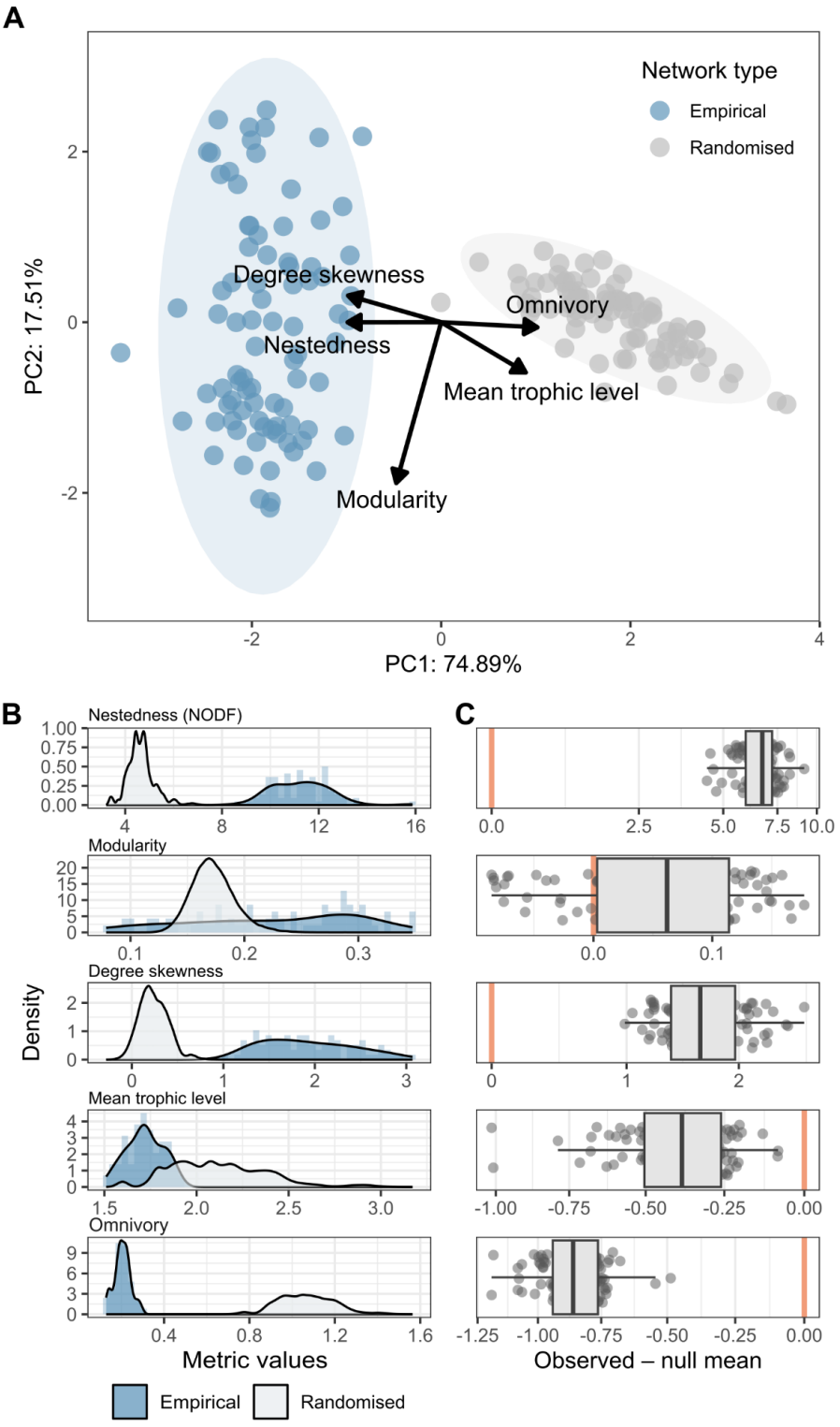


Figure S4. **Responses of network properties to local habitat quality and urban density.** Standardised coefficients (±95% CI) from linear models relating richness-based, compositional and structural metrics to local habitat quality (green) and urban density (brown), relative garden area (pink) and garden type (private, in comparison to allotment gardens). * indicates the usage of a z-score rather than the raw network metric. Points indicate model estimates; coloured symbols show significant effects (P < 0.05) and transparent symbols indicate non-significant effects.

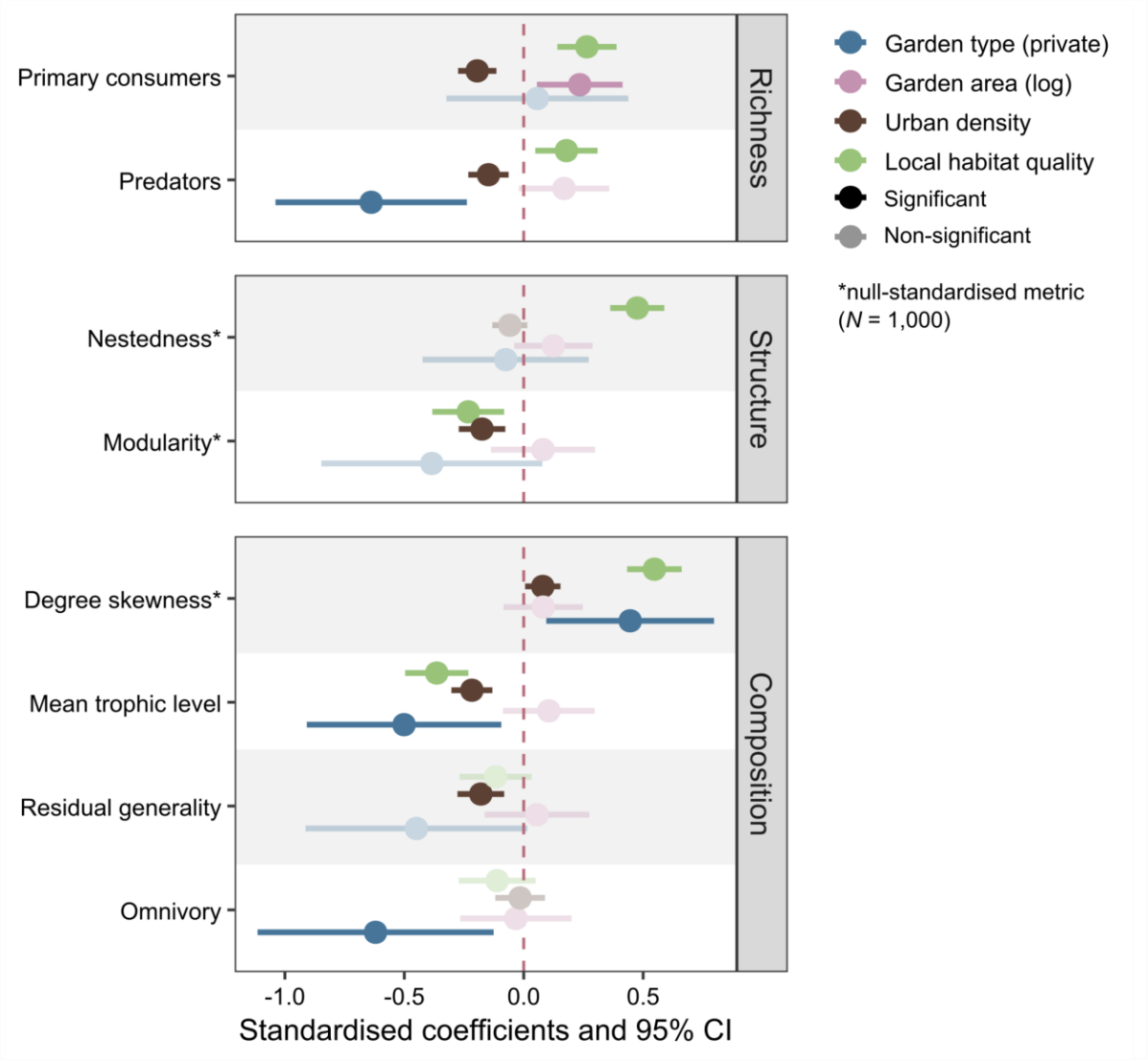


Figure S5. **Interaction model.**

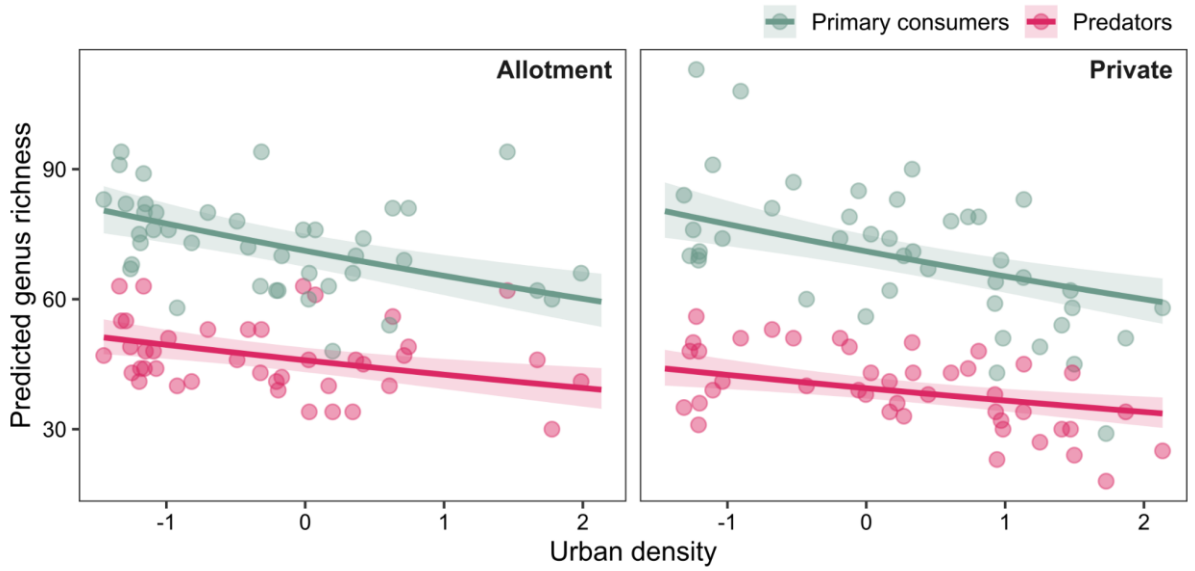


Figure S6. **Relationship between two complementary measures of food-web robustness under random-removal and sensitivity-based extinction scenarios.** Points represent individual gardens. Spearman rank correlations showed that their association was stronger under random (ρ=0.72, p < 0.001) than sensitivity-based removal (ρ=0.46, p < 0.001, Fig. S6). A paired bootstrap resampling confirmed a positive difference between correlations (Δρ=0.26, 95% bootstrap CI: 0.13–0.41, 10,000 replicates).

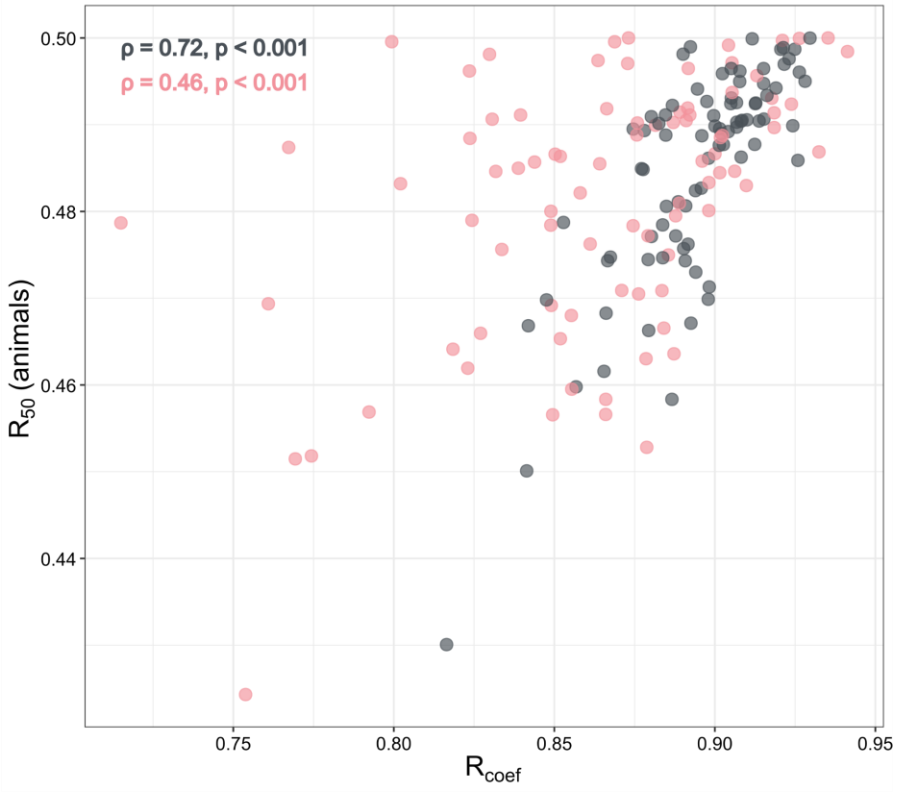


Figure S7. **Full model results for food-web robustness under random and urban-sensitivity extinction scenarios.** Coefficient estimates (±95% CI) from β-GLMMs testing the effects of urban density, local habitat quality, garden type, garden area and the interaction between urban density and local habitat quality on two robustness metrics: the robustness coefficient, R_{coef} and R_{50} of consumer taxa. Colours indicate extinction scenario: random removals and removals weighted by taxon sensitivity to urban density. Filled points indicate significant effects and open points indicate non-significant effects.

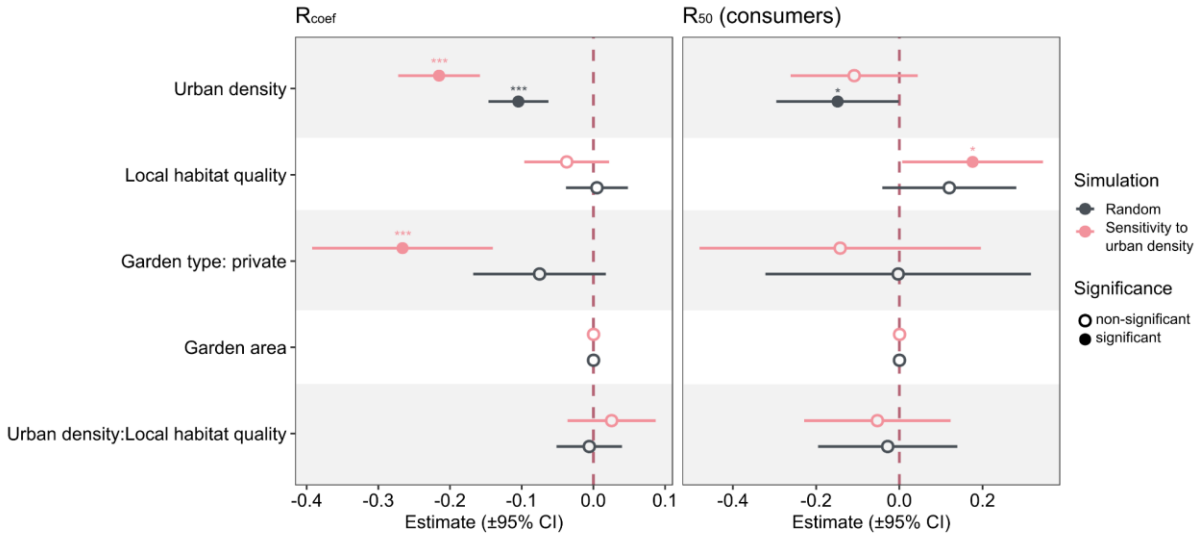


Figure S8. **Component models underlying the structural equation models.** Standardised coefficient estimates and 95% confidence intervals are shown for the individual linear submodels used in the piecewise structural equation models linking urban density, local habitat quality, predator richness, food-web structure, food-web composition and robustness. Panels show the response variable for each submodel. Blue and red points indicate significant positive and negative effects, respectively, while grey points indicate non-significant effects. Points represent standardised model estimates and horizontal bars represent 95% confidence intervals.

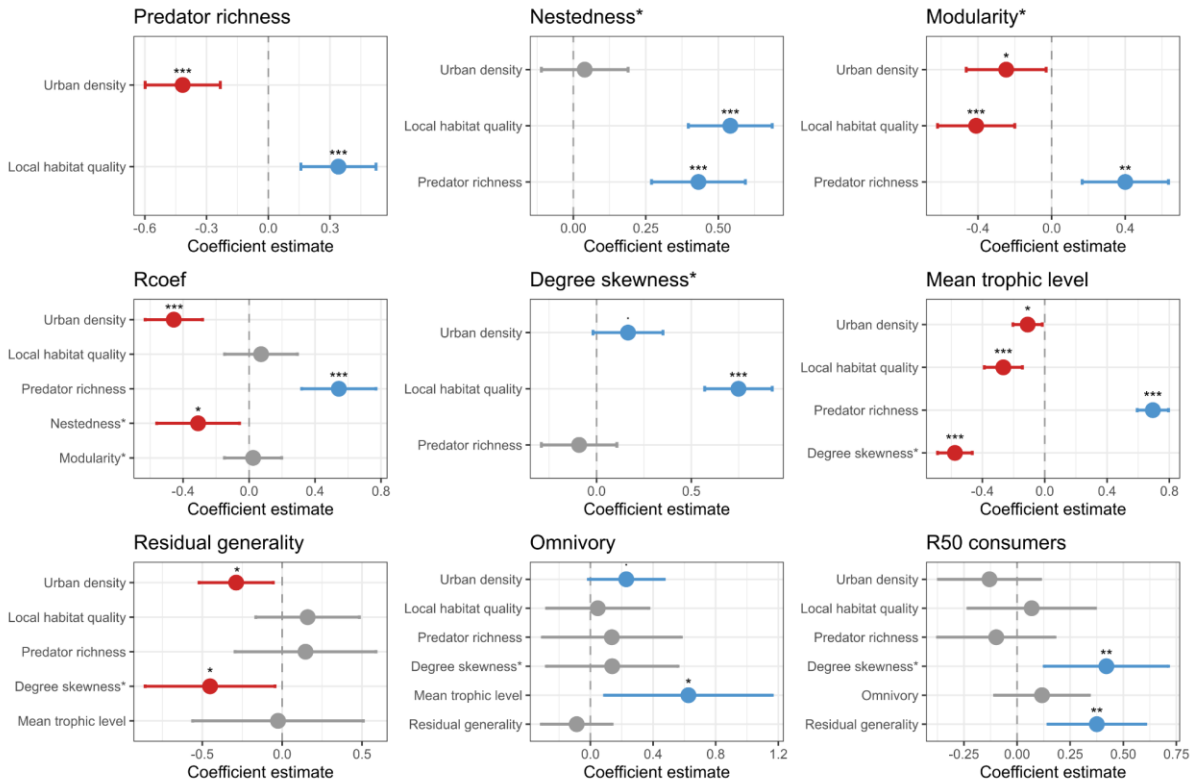


Figure S9. **Structural equation models linking urban density and local habitat quality with structural and compositional properties of garden food webs and robustness against the random removal of taxa.** Black arrows indicate positive effects and red arrows indicate negative effects (P < 0.05). Only significant relationships are presented. (A) Standardised path coefficients (|β| shown on arrows) describe direct relationships among predictors and compositional food-web metrics: degree skewness (z-score relative to null models), mean trophic level, residual generality (independent of richness), omnivory, and R_{50} threshold (consumers only). (B) Standardised path coefficients (|β| shown on arrows) describe direct relationships among predictors, predator richness, structural metrics: nestedness, modularity (all expressed as z-scores relative to null models) and the robustness coefficient R_{coef}. (C) Total, direct and indirect effects of urban density and local habitat quality on food web composition, structure, and robustness. Shapes indicate effect types (filled round for direct, open round for indirect, square for total), with lines representing 95% confidence intervals derived from bootstrapped standardised coefficients (10,000 resamples). Transparent points represent non-significant relationships.

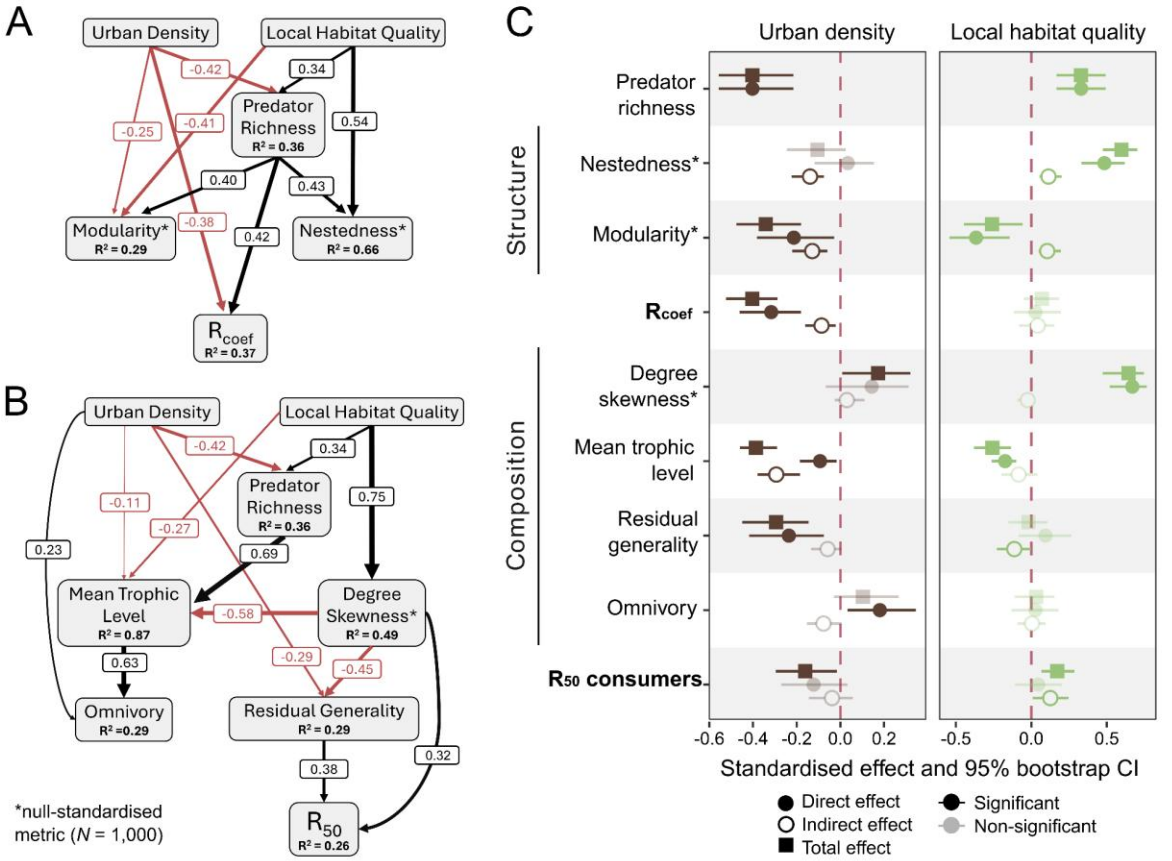
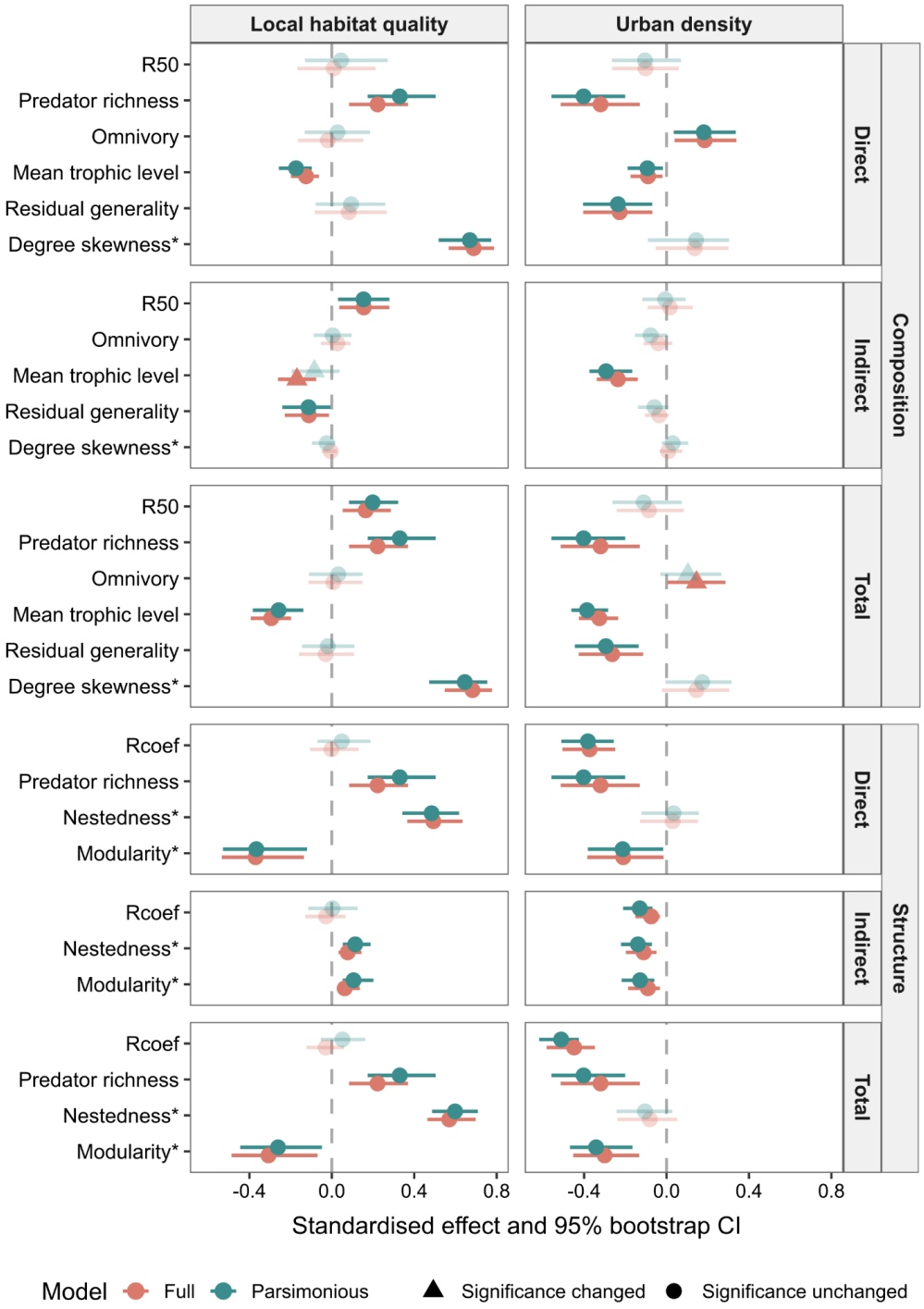


Figure S10. **Sensitivity of structural equation model estimates to the inclusion of garden area and garden type as covariates.** Direct, indirect and total standardised effects of local habitat quality and urban density are shown for the full SEMs including garden area and garden type and for parsimonious SEMs excluding these covariates. Points indicate effect estimates and horizontal lines show 95% bootstrap confidence intervals. Opaque symbols indicate effects whose confidence intervals did not overlap zero, whereas transparent symbols indicate non-significant effects. Triangles indicate effects for which statistical significance differed between the full and parsimonious models; circles indicate unchanged significance. Asterisks denote network metrics expressed as z-scores relative to null-model expectations.



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